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THE

AMERICAN NATURALIST

VOL. XXXV. *April, 1901.* NO. 412.

A THEORY OF THE ORIGIN AND EVOLUTION OF THE AUSTRALIAN MARSUPIALIA.

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INTRODUCTION.

ALTHOUGH considerable attention has been given to the discussion of the family and generic affinities of the Australian marsupials from a systematic standpoint, until very recently the phylogenetic aspects of the question have been generally neglected. On this account, and also from the fact that little information has been forthcoming either from paleontology or geographical distribution, it has not been possible, up to the present time, to form an adequate conception of the origin of the fauna and its phylogenetic relationships.

The present paper is the result of an attempt to outline a plan of evolution for the group by comparing the adaptive modifications of the teeth and feet with those of placental mammals, in which the course of evolution is fairly well known. On account of the difficulties with which the writer has had to contend in having only a small number of marsupial types at his disposal, the present plan is advanced simply as a working hypothesis. A fuller discussion of the question will be published in the course of a few months.

The fact was noticed long ago by Cuvier, and has been commented upon by many zoölogists since, that the marsupials of Australia assume much the same rôles in nature as are taken by placentals in other parts of the world, and that they show extensive resemblances to the latter in many features of their external organization. It is only within the last few years, however, in fact since the evolution of the placentals has come to be understood, that the exact significance of these resemblances has been at all apparent. Knowing that during the Tertiary period placental mammals have undergone a progressive development, or, in other words, an adaptive radiation, from diffuse or collective types, by which not only their minor but also their ordinal characters have been established, the question now suggests itself, Have not the Australian marsupials undergone an entirely similar or, in other words, a *parallel* radiation?

The possibility of such a condition has already been suggested by Osborn ('99a), who recognizes several mammalian radiations, including among them a marsupial radiation for Australia, and remarks as follows: "We mark the fact that the above radiations are all of ordinal rank, for the marsupial radii, although termed families, are adaptively equivalent to several placental orders."

Examining the composition of the group somewhat in detail, we find many indications of such a parallel radiation. Two classes of facts may be specially noticed in this connection. First, the Australian marsupials constitute a very homogeneous group; although differing widely in extremes, not only the various genera of a family but also the families themselves are connected by almost insensible gradations of structure. Second, the adaptive modifications of their teeth and feet are very similar to those of placental mammals either at the present day or during their progressive development in the Tertiary period, and they bear the same relation as do those of placentals to the general primitiveness of the animals in which they occur.

The Australian marsupials, therefore, show no signs of a composite structure such as might be expected if they represented migrated portions of the fauna of another continent, or, again, if they were of polyphyletic origin. Except in a very few instances, they show no signs of degeneration; as a group they are, like the placentals, progressive throughout. In short, the only satisfactory explanation that can be given for the homogeneous character of the group and their adaptive resemblances to placentals seems to be that they have undergone an entirely similar radiation under similar conditions, that it has proceeded from a single sharply marked ancestral type, and that the center of radiation has been the Australian region itself.

Assuming that a similar radiation has taken place in marsupials and placentals, it will be apparent that a plan of evolution may be constructed for the former by inference from that of the latter. Thus, by noting the sequence of events in the development of the adaptive modifications of the teeth and feet in placentals during the Tertiary period, we may infer a similar sequence in those of marsupials, and in this way determine their probable course of evolution in these structures, and also the characters of their stem form.

THE PROBABLE CHARACTERS OF THE MARSUPIAL STEM FORM.

Dentition. — In the case of the placental mammals, progressive evolution in dentition is accompanied by a reduction of certain of the teeth and by an elaboration of certain others, notably the molars. Unreduced dentitions with slightly elaborated teeth are therefore primitive. But just as in formulating such a law it is necessary to exclude those forms whose dentition, while being of primitive aspect, is not typically primitive, but primitive through degenerate specialization (Delphinidæ, Otariidæ), it is also necessary in applying it to the case of the marsupials to exclude similarly conditioned forms of that series.

The only marsupials which call for consideration in this respect are the forms Myrmecobius and Notoryctes.[1] There are two reasons for regarding these as degenerate in dentition. First, there is a prototypal tooth pattern in marsupials, which is shared alike by the Didelphyidæ and the insectivorous members of the Dasyuridæ, and of which the tooth patterns of the carnivorous Dasyuridæ and the Peramelidæ are undoubtedly progressive modifications, while those of Myrmecobius and Notoryctes are aberrant. The tooth patterns of both of these forms are more primitive in aspect than those of any other of the Australian forms, but the animals are specialized in other respects. Thus Myrmecobius is typically dasyurid in foot structure and in its incisor formula of $\frac{4}{3}$, while Notoryctes, according to Dollo (**'99**), is specialized in a phalangerine direction in foot structure. Second, both Myrmecobius and Notoryctes are ant-eating forms,[1] such animals being usually degenerate in dentition, judging from Echidna and the placental Myrmecophagidæ and Manidæ, in which the teeth have been entirely lost.

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[1] Tarsipes appears to be degenerate in dentition, but the teeth are not primitive in aspect.

Excluding Myrmecobius and Notoryctes, we find the primitive dental characters of marsupials distributed as follows :

The least reduced dentition is found in the Peramelidæ, where the formula is : $i.\frac{5}{3}$, $c.\frac{1}{1}$, $p.\frac{3}{3}$, $m.\frac{4}{4}$.[2]

The least elaborated molar teeth are found in the insectivorous members of the Dasyuridæ. The upper teeth (Pl. I, Fig. *d*)[3] are triangular in shape, with three main cusps (protocone, paracone, metacone)[4] and an outer row of styles. There are no conules at the base of the protocone, such as are commonly met with in placental types. The metacone exceeds the paracone in size, and its posterior border is produced into a trenchant spur. The lower teeth (Pl. II, Fig. *d*) are of the tubercular sectorial pattern, with a main triangle bearing three cusps (protoconid, paraconid, metaconid) and an antero-external shelf, and a posterior heel bearing one outer (hypoconid) and two inner (entoconid and hypoconulid) cusps.

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[1] For habits of Notoryctes see Stirling (**'91**, p. 158) and Spencer (**'96**, p. 50, Mammalia).

[2] Or $(m)i.\frac{5}{3}$, $mc.\frac{1}{1}$, *mp.* and $pp.\frac{4}{4}$, $m.\frac{3}{3}$, following Lydekker (**'99**). The upper incisor dentition may contain teeth of both series.

[3] This type might be more appropriately illustrated by the teeth of Phascologale, Sminthopsis, or Antechinomys, *Dasyurus viverrinus* being more carnivorous in habit. Thomas, however, remarks that the teeth of the three former genera resemble one another very closely, and differ only from those of Dasyurus in being more acutely cuspidate. See Thomas (**'88**, pp. 273, 298, 309).

[4] Following the nomenclature of the tritubercular theory. See Osborn (**'88**, **'91**).

Foot Structure.[1] — In placental mammals, progressive evolution in foot structure, beautifully illustrated in Tertiary Ungulata, is accompanied by a reduction of certain of the digits, and by an elaboration of certain others, the evolution proceeding from an ideal pentadactyl condition, such as is seen typically in the Eocene Creodonta. Among the Australian marsupials the nearest approach to the ideal pentadactyl type is seen in certain members of the Dasyuridæ (Pl. III, Fig. *d*). The hallux is opposable but slightly reduced, while the remaining digits are normal.

Summing up the above results, we may make the general statement that the marsupial stem form possessed the following characters, or more primitive ones: Dental formula, $i.\frac{5}{3}, c.\frac{1}{1}, p.\frac{3}{3}, m.\frac{4}{4}$. Upper molar teeth triangular, with three main cusps and an outer row of styles; metacone exceeding paracone, its posterior border produced into a trenchant spur; no conules at the base of the protocone. Lower teeth with anterior triangle bearing three cusps and an antero-external shelf, and posterior heel bearing one outer and two inner cusps. Foot with hallux completely opposable, the remaining digits normal.

The fact will now be apparent that the above prototypal characters are not found associated in any Australian form. All of the Australian marsupials are derived types. On the other hand, with one exception they are all found in the American Didelphyidæ. The one exception refers to the presence in the latter of four instead of three lower incisors, and in this respect the Didelphyidæ are more primitive. The molar tooth patterns of the stem form are almost exactly reproduced in those of the Oligocene Opossums (Peratherium) (Pls. I and II, Fig. *a*).[2]

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[1] This refers throughout to the pes in the case of the marsupials.

[2] In the specimen from which these diagrams were taken (*Peratherium fugax* Cope) the outer parts of the upper molars are worn, so that, although there is a conspicuous external ridge, the presence of styles cannot be affirmed. *Cf.* Cope (**'84**, Pl. LXII, Fig. 2*a*).

As regards the modifications of the teeth and feet, therefore, the Didelphyidæ exhibit characters which are ancestral to those of the Australian marsupials. The question now arises as to whether or not they are ancestral in other respects. The opportunity has not yet presented itself to the writer of examining the case in detail, so that only a few examples will be given here. As was pointed out in 1880 by Brass, the complex modifications which result in the formation of the peculiar median vagina in specialized marsupials are seen in their incipient stages in the Didelphyidæ, where the two vaginæ bend toward one another in the middle line. Passing onwards from the Didelphyidæ every gradation is met with, until the final stage is reached in the Macropodidæ.

Again, taking the case of the marsupium, the anteriorly directed opening of this structure, as seen in the Phalangeridæ and Macropodidæ, and the posteriorly directed opening, as seen in the Peramelidæ and Notoryctidæ, are obvious departures from such a type as is seen in the Didelphyidæ and Dasyuridæ, in which the opening is directed vertically downwards.

Finally, taking the case of the tail, which is an adaptive structure of the greatest importance in marsupials, it is entirely probable that the hairy, non-prehensile condition, where it occurs in the Australian forms, has been derived from a naked, scaly, prehensile one, such as is seen in the Didelphyidæ. Thomas (**'88**) describes for the Dasyuridæ, in which the tail is hairy and never prehensile, a scaly condition in various genera, among them *Phascologale wallacei*, *P. flavipes*, and *Sminthopsis leucopus*. A scaly tail, which, according to Thomas, is said to be also prehensile, is found in *Perameles broadbenti* among the Peramelidæ. Every grade of prehensilism is met with among the Phalangeridæ; and, finally, among the Macropodidæ, a scaly tail is found in *Hypsiprymnodon moschatus*, and a prehensile one in the various species of Bettongia.

The above facts, when added to the evidence of the teeth and feet, suggest strongly a former connection of the Didelphyidæ with the Australian marsupials, and although, in attempting to express such a connection phylogenetically, it is a natural procedure to regard the original members of each group as the descendants of a common stock, the Didelphyidæ are so primitive that it is scarcely possible to regard them, as a family, otherwise than ancestral.[1]

THE EVOLUTION OF THE TEETH IN AUSTRALIAN MARSUPIALS.

It has already been mentioned that progressive evolution in dentition, in the case of the placental mammals, is accompanied by a reduction of certain of the teeth and by an elaboration of certain others, notably the molars. The researches of Cope, Osborn, and others have shown that in the evolution of the molar teeth the elaboration proceeds from a trituberculate condition in the upper series, and from a quinquetuberculate or sexituberculate condition in the lower series. These types are exemplified in the teeth of the primitive Creodonta of the early Eocene (Protochriacus, Oxyclænus, etc.).

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[1] This involves the question of the limitations of the family Didelphyidæ. Lydekker (**'96**, p. 109), while assigning the didelphyid incisor formula to the ancestors of the Dasyuridæ, speaks (p. 55) of the Didelphyidæ and Dasyuridæ as descendants of a common stock. Spencer (**'96**, p. 188, Summary) speaks of a primitive (South American) group giving rise to the Didelphyidæ of America on the one hand, and to the early Australian types on the other. Ameghino (**'93**, p. 16) regards the family called by him Microbiotheriidæ as ancestral to the Didelphyidæ and to the Australian Dasyuridæ. In the writer's opinion it will not be found advisable ultimately to regard the Didelphyidæ as a modern derived group, but that, when the actual ancestors of the Australian forms are identified, it will probably be found necessary to extend the family Didelphyidæ to include them. Two reasons for this view may be noted. First, the Oligocene forms of Europe and North America have already been included in the existing American family; in other words, we identify as Didelphyidæ forms which existed at about the time when the Australian fauna probably arose. Second, the family Didelphyidæ, as at present limited, is not equivalent to any one of the four typical families of Australian marsupials, the latter being much more comprehensive. The diversity of organization which is met with among the Dasyuridæ in the genera Phascologale and Thylacinus, among the Phalangeridæ in the genera Phalanger, Phascolarctos, and Tarsipes, among the Macropodidæ in the genera Hypsiprymnodon and Macropus, is absolutely without parallel among the Didelphyidæ. If, therefore, the integrity of the Australian families is to be retained, — and there is every reason for believing that they are natural groups, — there are good grounds for extending the family Didelphyidæ to include their own ancestors and those of the Australian forms, if the latter, as they probably did, possessed the main didelphyid modifications of the teeth and feet, even while differing in other minor details. The Microbiotheriidæ of Ameghino may be a case in point.

From this point onwards development takes place along two main lines. In one case the outer cusps of the teeth from being tuberculate become laterally compressed and trenchant, giving rise to the carnivorous modification, seen typically in the specialized Creodonta (Oxyæna, Hyænodon, Oxyænodon, etc.). In the other case the primitive tooth pattern is entirely changed; the upper teeth become quadritubercular by the addition of a postero-internal cusp (hypocone), while the lower teeth also become quadritubercular by the reduction of the most anteriorly placed cusp (paraconid), and the intermediate cusp of the heel (hypoconulid). In this way a primarily omnivorous modification is instituted, which is seen in its constructive stages in the Eocene Condylarthra (series Protogonodon, Euprotogonia, Phenacodus, and various separate genera).

From the typically quadrituberculate condition evolution proceeds in two directions, both leading to the herbivorous modifications of the Ungulata. In one series the cusps of both upper and lower teeth become crescentic, producing the condition characteristic of the Artiodactyla; while in the other they become lophoid, producing the complex modifications of the Perissodactyla. The latter evolution is beautifully illustrated in passing from the Eocene genera (Hyracotherium, Systemodon, etc.) to the modern types.

If, now, we arrange the teeth of the Australian marsupials according to the above placental plan, we obtain such a result as is represented diagrammatically in Pls. I and II. The primitive trituberculate, tubercular sectorial type is here represented by the teeth of *Dasyurus viverrinus* (Fig. *d*). As indicated elsewhere in a footnote, this would be more appropriately illustrated by the teeth of one of the purely insectivorous forms of the Dasyuridæ (Sminthopsis, Antechinomys, Phascologale).

The carnivorous line above mentioned is, in the case of the Australian marsupials, entirely confined to the family Dasyuridæ, and it culminates in the Tasmanian wolf (*Thylacinus cynocephalus*). The teeth of this animal are represented in Pls. I and II, Fig. *g;* they show all the essential characters of those of Dasyurus, except that in the lower teeth the metaconid is absent. The progressive carnivorous modification is, in the upper molars, a conversion of the paracone and metacone into cutting blades, and a reduction of the outer styles, which are here represented by very inconspicuous tubercles. In the lower teeth the progressive modification is a conversion of the paraconid, protoconid, and hypoconid into cutting blades, and a reduction of the metaconid, hypoconulid, and entoconid.

Turning to the second stem, leading to the omnivorous and herbivorous modifications, we find the first stage represented in the teeth of the Peramelidæ. The upper molars of *Perameles nasuta* (Pl. I, Fig. *c*) show all the essential characters of those of Dasyurus, but in addition they show an incipient hypocone. In the third molar the hypocone is not very pronounced, and the tooth is triangular; but in the second molar the hypocone is well developed, and the tooth is now quadrate. Thomas ('88, p. 220) describes the triangular and quadrate modifications as characteristic of the family. The upper molars of the Peramelidæ parallel, in a general way, those of the Condylarthra above mentioned. The lower molars of *Perameles nasuta* (Pl. II, Fig. *e*) resemble still more closely those of Dasyurus, the omnivorous modification being only apparent in the posterior heel, where the hypoconulid is reduced.

The completed omnivorous modification is doubtless to be met with in the Phalangeridæ. Unfortunately, only two examples of this family have been available to the writer, namely, *Trichosurus vulpecula*, which is highly specialized, and *Petauroides volans*. The teeth of the latter animal are represented in Pls. I and II, Fig. *f*. Although they illustrate the completed quadrituberculate condition, they are only approximately transitional; the hypocone is completely formed in the upper molars, and the paraconid is reduced in the lower molars; but the antero-external shelf, which is prominent in the lower teeth of the Peramelidæ and Dasyuridæ and very conspicuous in those of the Macropodidæ (Pl. II, Fig. *i*), is here absent, and there are no traces of external styles in the upper teeth.

The selenoid modification of the cusps, which is so widely represented in the artiodactyl Ungulata, appears to be confined to the single form Phascolarctos (Pls. I and II, Fig. *j*) among the marsupials, but the lophoid modification is widely represented in the Macropodidæ (Pls. I and II, Fig. *i*). The incipient stages are seen in the teeth of the specialized Phalanger, *Trichosurus vulpecula* (Pls. I and II, Fig. *h*), and also in those of *Hypsiprymnodon moschatus* (Macropodidæ). It is of interest to note that the lophoid modification is accompanied by a hypsodont condition of the crown in the Macropodidæ, as in the perissodactyl Ungulata.

THE EVOLUTION OF THE FEET IN AUSTRALIAN MARSUPIALS.

It was pointed out by Huxley in 1880 that none of the Australian marsupials possess a normal pentadactyl pes, that wherever the hallux is present it presents an extensive movement of adduction and abduction ; in other words, that the marsupial foot is typically prehensile.

Quite recently a careful study of the foot structure of marsupials has been made by Dollo ('99), who endeavors to demonstrate a derivation of all recent forms from arboreal ancestors. Dollo has indicated all the important adaptive modifications in Australian marsupials, although he has not discussed their phylogenetic significance, so that all that is necessary in the present paper is to arrange his types into a phylogenetic series, in accordance with his interpretations and the general plan noted above for the placentals.

Dollo has shown that the arboreal marsupials present successive stages of arboreal adaptation, following which the foot becomes more and more modified. Thus, beginning with the Didelphyidæ (Pl. III, Fig. *a*), the foot is provided with an opposable hallux, and the remaining digits are normal. In the Phalangeridæ (Fig. *b*) the hallux is again opposable, but in addition the fourth digit is enlarged, and the second and third are reduced and syndactylous. Finally, in one member of the Phalangeridæ, Tarsipes (Fig. *c*), there is, in addition to all of these arboreal characters, a recession of the claws of the fourth and fifth digits. It is thus possible to recognize an arboreal line of evolution such as is represented in Pl. III, *a–c*.

Among the terrestrial or semi-terrestrial marsupials, all of the forms, except the specialized members of the Dasyuridæ, show some of these arboreal characters, indicating that up to a certain stage they have been arboreal in habit. It is thus a simple matter to arrange them in collateral groups according to the stage at which their terrestrial evolution began. Such an arrangement as this is represented diagrammatically in Pl. III, in the side lines passing off from the main arboreal line *a–c*. The first series to be given off is that of the Dasyuridæ. In the least modified members of this family the animals are still arboreal, and the foot (Fig. *d*) is like that of Didelphys (Fig. *a*), except that the hallux is slightly reduced. As Dollo has pointed out, it is possible to recognize a complete series here, following which the hallux becomes gradually reduced and finally obliterated (*e*).

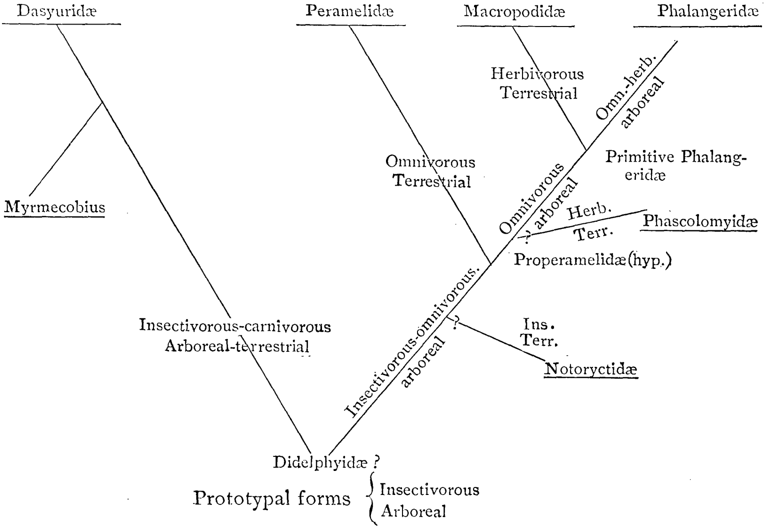
Two other terrestrial offshoots, which parallel one another, and arise from the main arboreal line at the phalangerine stage, are represented by the Peramelidæ and Macropodidæ. In both of these the evolution is cursorial as well as terrestrial, and is accompanied by a reduction of the hallux and an enormous enlargement of the fourth digit, so that the foot becomes functionally monodactyl. The extremes of structure in these lines are, as Dollo has indicated, in the Peramelidæ *Perameles doreyana* (Fig. *g*) and *Peragale leucura* (Fig. *h*) and in the Macropodidæ *Hypsiprymnodon moschatus* (Fig. *i*) and Macropus (Fig. *j*).

Another terrestrial offshoot is represented by the Phascolomyidæ (Fig. *f*), although the relations of this branch are doubtful. The hallux is reduced in these animals as in other terrestrial forms. With respect to the remaining digits, the foot appears to be transitional between that of the Didelphyidæ and that of the Phalangeridæ, the second and third digits not being so reduced as in the latter family. The difficulty arises here as to whether or not the second and third digits, from being fully reduced, as in the Phalangeridæ, have been secondarily enlarged. Such a condition would appear to be not improbable in slow-moving animals, such as the wombats ; in the other animals which have passed through a phalangerine stage the tendency towards monodactylism has doubtless prevented the second and third digits from becoming secondarily functional.

For Notoryctes Dollo describes a slight syndactylism and reduction of the second and third digits, which points out this form as still another offshoot of the main arboreal line.

GENERAL REMARKS ON THE EVOLUTION OF AUSTRALIAN MARSUPIALS.

When we compare the plan of evolution as determined by the structure of the teeth with that determined by the structure of the feet, we note the fact that they practically coincide. Thus there are two lines leading from the prototypal forms, one of them showing an insectivorous-carnivorous and an arboreal-terrestrial evolution leading to the Dasyuridæ, the other showing an insectivorous-omnivorous and a progressive arboreal evolution leading to all the remaining marsupial families.



Following the former line, there appears to have been a typical evolution in all forms except Myrmecobius, which, as noted above, is probably degenerate in dentition.

Following the omnivorous arboreal line, we find that one of its stages has been obliterated, being unrepresented among existing forms. The characters of other forms, however, leave no doubt as to its composition. Thus the Phalangeridæ present a typical arboreal modification of the foot, combined with advanced omnivorous and herbivorous modifications of the teeth, while the Peramelidæ present a terrestrial modification of the phalangerine foot, combined with a primitive omnivorous condition of the teeth. There must, therefore, have existed at some time, if the present plan is reliable, a series of forms such as is represented in the general diagram on p. 256 as Properamelidæ (hyp.), consisting of animals which combined a phalangerine type of foot with a primitive omnivorous dentition. These animals would have given rise to the Peramelidæ by a terrestrial modification of the foot, and to the Phalangeridæ by a more completely omnivorous and finally herbivorous modification of the teeth.

From the phalangerine stem, after the omnivorous modification was established, there was apparently given off a branch to the Macropodidæ, with a trend of evolution from arboreal to terrestrial, and from omnivorous to herbivorous. The herbivorous modification reaches its greatest development in this family.

The phylogenetic positions of the Phascolomyidæ and Notoryctidæ, as indicated in the general plan, are by no means certain. In the case of the former, the difficulty in interpreting the foot structure has already been commented upon. The unworn molar teeth of these animals are said by Krefft ('75) to be quadrituberculate. If such is the case, it would appear probable that they arose from the omnivorous arboreal stem after the Peramelidæ were given off, and that there has been a secondary enlargement of the second and third digits.

In the case of the Notoryctidæ the writer has not been able as yet to decide definitely the cusp homologies in the upper teeth, but the lower are undoubtedly tritubercular; as indicated above, the dentition is probably degenerate. Combining this interpretation with the evidence of arboreal characters in the foot, it would seem probable that Notoryctes arose from the arboreal omnivorous line somewhere near the Properamelidæ.

A DIDELPHYID ORIGIN IN THE LIGHT OF GEOGRAPHICAL DISTRIBUTION.

In discussing the question of the origin of the Australian marsupials it is apparent that, apart from the evidence derivable from the organization of existing types, any opinions which are expressed on the subject must take into consideration the present and past geographical distribution of marsupials, the manner in which the ancestral forms gained access to the Australian region, and the time at which their entry was effected.

Within the last twenty-five years several attempts have been made to connect the Australian marsupials with the extinct types of different horizons in other countries, and to explain in this way the conditions of their origin. Thus, in 1876, Wallace suggested a possible relation to the Jurassic forms of the northern hemisphere.[1] Concerning this he speaks as follows: "As, however, no other form but that of the Didelphyidæ occurs there (in Europe) during the Tertiary period, we must suppose that it was at a far more remote epoch that the ancestral forms of all the other marsupials entered Australia; and the curious little mammals of the Oölite and Trias offer valuable indications as to the time when this really took place."[2] . . . "It was probably far back in the Secondary period that some portion of the Australian region was in actual connection with the northern continent, and became stocked with the ancestral forms of marsupials."[3]

In 1882 Cope, in commenting upon the ancestry of Thylacoleo, placed this form in the family Plagiaulacidæ of the northern hemisphere, and regarded the latter as related to the Australian Macropodidæ through a hypothetical ancestor Tritomodon. There is, however, no valid evidence in favor of this view.

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[1] Haeckel has recently endeavored to express such a relation phylogenetically by deriving all of the modern marsupials from a Jurassic group of Prodidelphia, which he regards as also ancestral through certain of its members, the Amphitherida and Amblotherida, to the placentals. See Haeckel (**'95**, p. 471).

[2] Wallace (**'76**, vol. ii, p. 253).

[3] *Ibid.* (vol. i, p. 465).

By far the most complete discussion of the question, from all points of view, is that given by Lydekker ('**96**) in his *Geographical History of Mammals*. Lydekker, while agreeing with Wallace as to the northern origin of the Australian fauna, fixes its time of entry at a much later period, namely, at the beginning of the Eocene, on the basis of a possible connection of the ancestors of the Australian Dasyuridæ with those of the Oligocene Didelphyidæ of the northern hemisphere. He remarks as follows (p. 55): "Recent researches have tended to show that the alliance between the Dasyuridæ and the Didelphyidæ is much more intimate than was formerly supposed to be the case. This being so, it is a fairly safe assumption that both families are descended from a single common ancestral stock." . . . "Not improbably polyprotodont marsupials survived in southeastern Asia till the early portion of the Eocene division of the Tertiary epoch, and in this region both Dasyuridæ and Didelphyidæ were differentiated. Representatives of the former family soon afterwards found their way into Australia and New Guinea, while the opossums would appear to have dispersed in one direction into Europe and in the other into North America."

Objection has been taken to this view by Spencer ('**96**) on account of the difficulty of explaining by it the non-appearance of Didelphyidæ in Australia and the paucity of polyprotodont types in New Guinea, and also on account of the lack of evidence of the former presence of marsupials in Asia.

For a northern origin Spencer substitutes a South-American one taking place in the late Cretaceous through the medium of an Antarctic continent. This idea is also favored by P. L. and W. L. Sclater ('**99**). Viewing the question from a phylogenetic standpoint alone, Lydekker has recently ('**99**) suggested the Prothylacinidæ (Sparassodonta of Ameghino) of the South-American Miocene as possibly ancestral to the Dasyuridæ, and Ameghino ('**93**) regards the family called by him Microbiotheriidæ as ancestral to both the Dasyuridæ and the Didelphyidæ.

Spencer, however, in attempting to derive the Australian fauna, encounters the same difficulty which confronted Lydekker, namely, how to explain the non-appearance of Didelphyidæ in Australia. Concerning this he remarks as follows (p. 188, Summary): "The only way in which it seems possible to account at once for the presence of forms such as Prothylacinus in the Patagonian Tertiary beds, and the absence of any of the Didelphyidæ in Australia, is to suppose that on the South-American side the connection between the Antarctic land and what is now Patagonia was lost at a time comparatively soon after the early polyprotodonts had passed across, and during which the Didelphyidæ were being developed perhaps in the more northern part of South America."

In the writer's opinion, the difficulty of explaining the absence of the Didelphyidæ from Australia is only an apparent one, which is due to the interpretation of this family as a modern derived group. Reasons have already been given for the elevation of the family to an ancestral position, and if the case is susceptible of proof, no other explanation is necessary to account for their absence from the Australian region than the assumption that they were formerly present and subsequently disappeared. If we imagine the family to have originally gained access to the region, it is not difficult to conceive that, in establishing the foundations of an extremely comprehensive adaptive radiation, especially under the favorable conditions of absolute freedom from competition, they should have thrown aside their distinctive didelphyid characters. And more especially is this conceivable when we realize that the differences of structure separating the Didelphyidæ from the most primitive of the Australian forms (insectivorous Dasyuridæ) are very slight.[1]

Concerning the direction from which the ancestral Didelphyidæ may have entered the Australian region, there is at least some justification for the view that it was from the northward. Lydekker (**'96**, p. 57) has called attention to the fact that there are marked indications of a faunal affinity of North America and Asia, which points to an interchange of forms between the two continents. This suggests a connection of the Oligocene opossums of Europe with those of North America, and, as Lydekker has pointed out, there may have been a migration of these animals into both countries from a common center in Asia ; on the other hand, there may have been simply a passage of forms *via* Asia. In either case the former presence of opossums on the latter continent would be indicated.

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[1] *Cf.* Thomas (**'88**, p. 315).

However this may be, the actual evidence at our disposal is very slight, and it is equally conceivable that ancestral Didelphyidæ may have entered by way of Antarctica. This possibility has been suggested by Osborn ('99b), although no preference is indicated by him for either view. As already indicated, the time at which the ancestral marsupials gained access to the Australian region has been estimated by Wallace as "far back in the Secondary," by Spencer as Cretaceous, and by Lydekker as early Eocene. It is probable, however, that these estimates are much too great, and that the time of entry was considerably later. Comparing the marsupial and placental radiations with respect to the modifications of the teeth and feet, we notice the fact that while there is a general correspondence between the most primitive characters of each series, there is no such correspondence between the most specialized ones. The most specialized characters of marsupials are decidedly primitive as compared with the most specialized characters of placentals. To illustrate the case, while the insectivorous members of the Dasyuridæ and the Didelphyidæ approach closely the trituberculate pentadactyl ancestors of the placentals, the Macropodidæ, which are the most specialized of the marsupials, are much more primitive than the most specialized placentals (perissodactyl Ungulata) whose evolution they parallel. The lophiodont teeth of these forms are very similar to those of such persistent primitive types as the Tapiridæ and their immediate ancestors, having none of the complex characters of those of the progressive lophiodont forms (Equidæ and Rhinocerotidæ). The functionally monodactyl, cursorial feet of the Macropodidæ are primitive as compared with the similarly modified feet of the Equidæ. Further, there is the remarkable fact that while the marsupial families have the value of placental orders, it is barely possible to separate them sharply as families. In fact, they show such a composition as must have existed at some stage of the placental radiation.

Now the Macropodidæ show no signs of being persistent primitive types, and there seems to be no valid reason for assigning to the marsupials a different potential of evolution. The only explanation which may be given for the above facts is, therefore, that the Australian radiation has been of comparatively short duration.[1] And if the placental radiation began in the late Cretaceous or in the early Eocene, as now appears probable, it is unlikely that the marsupial radiation can have begun until well on into the Tertiary. An ancestral association with the Oligocene opossums of the North or even with the Lower Miocene forms of South America is thus not improbable.

As to whether or not the ancestral forms gained access to the Australian region by means of a land connection would appear to be a matter of little consequence if the fauna is of didelphyid origin. Such minute animals as they must have been, judging from the Oligocene forms of the northern hemisphere and the diminutive opossums of South America, might have gained access to the region by transportation in various ways.

In conclusion, the writer wishes to acknowledge his indebtedness to Professor H. F. Osborn of Columbia University for many kind suggestions during the preparation of this paper, and to Professor Allen of the American Museum of Natural History, New York, Professor W. B. Scott of Princeton University, and Professor R. Ramsay Wright of the University of Toronto, for the privilege of examining the marsupial collections of the above-named places.

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[1] This suggests Huxley's statement of twenty years ago: "And I suspect that most, if not all, of the Australian forms are of comparatively late origin." (On the Application of the Laws of Evolution, etc., *P. Z. S.* (1880), p. 656).

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EXPLANATION OF PLATE I.

Illustrating the patterns of the upper molar teeth in marsupials and their probable phylogenetic relations.

NOTE. — The prototypal form is provisionally represented by Peratherium. Figs. b and c are inserted for comparison.

a. — *Peratherium fugax* Cope.
b. — *Didelphys azaræ* Temm.
c. — *Didelphys virginiana* Kerr.
d. — *Dasyurus viverrinus* Shaw.
e. — *Perameles nasuta* Geoff.
f. — *Petauroides volans* Thos.
g. — *Thylacinus cynocephalus* Fisch.
h. — *Trichosurus vulpecula* Jent.
i. — *Macropus sp.*
j. — *Phascolarctos cinereus* Fisch.

Abbreviations.

Pr. — protocone.
Pa. — paracone.
Me. — metacone.
Hy. — hypocone.
St. — external styles.

FIG. b, after Giebel (*Odontographie*, Taf. XVII, Fig. 10, *a*).

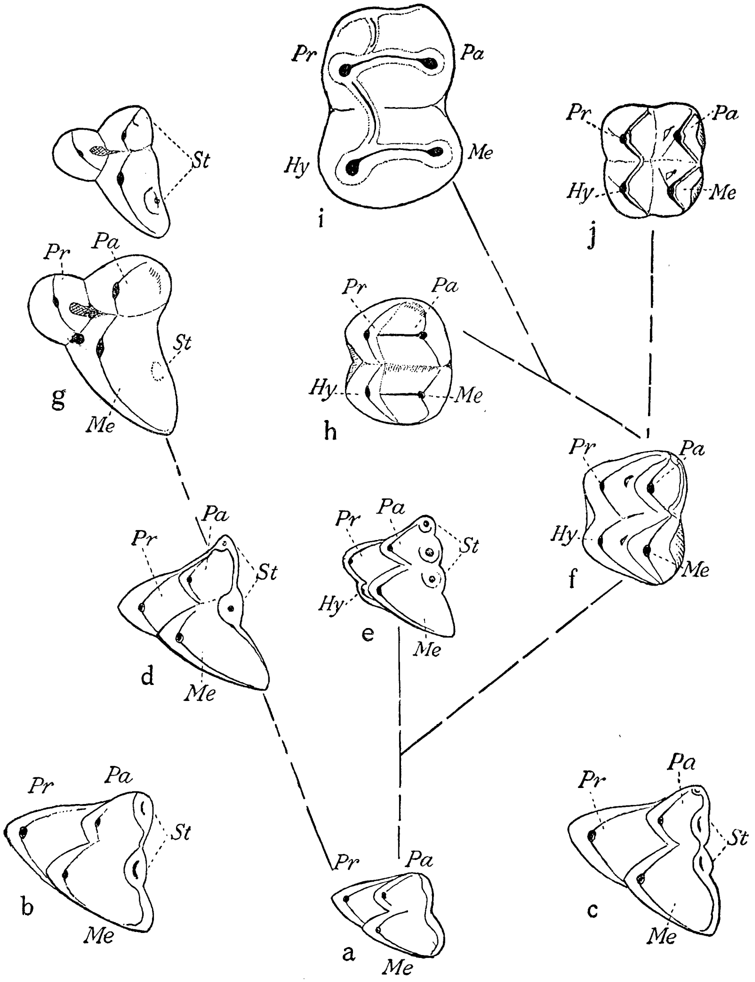

Pr
Pa
Hy
Me
i
St
Pr
Pa
Hy
Me
j
Pr
Pa
St
g
Me
Pr
Pa
Hy
Me
h
Pr
Pa
Hy
f
Me
Pa
Pr
St
d
Me
Pr
Pa
St
Hy
e
Me
Pr
Pa
St
b
Me
Pr
Pa
a
Me
Pr
Pa
St
c
Me

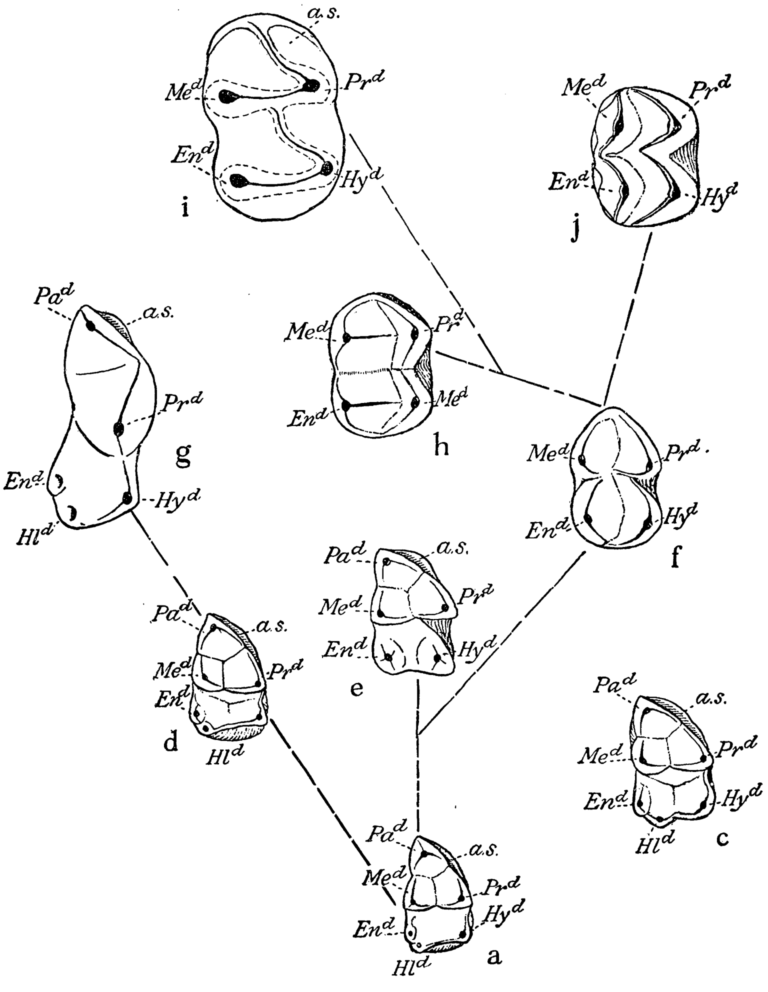
PLATE I.

EXPLANATION OF PLATE II.

Illustrating the patterns of the lower molar teeth in marsupials. (Same references as in Plate I.)

Abbreviations.

Pr^d. — protoconid.
Pa^d. — paraconid.
Me^d. — metaconid.
En^d. — entoconid.
Hy^d. — hypoconid.
Hl^d. — hypoconulid.
a.s. — antero-external shelf.


a.s.
Me^d
Pr^d
En^d
Hy^d
i
Me^d
Pr^d
En^d
Hy^d
j
Pa^d
a.s.
Pr^d
g
En^d
Hy^d
Hl^d
Me^d
Pr^d
En^d
Me^d
h
Me^d
Pr^d.
En^d
Hy^d
f
Pa^d
a.s.
Pr^d
Me^d
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Hy^d
e
Pa^d
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Me^d
Pr^d
En^d
d
Hl^d
Pa^d
a.s.
Me^d
Pr^d
En^d
Hy^d
Hl^d
c
Pa^d
a.s.
Me^d
Pr^d
Hy^d
En^d
Hl^d
a

PLATE II.

EXPLANATION OF PLATE III.

Illustrating the modifications of the pes in Marsupials and their probable phylogenetic relations.

a. — *Didelphys nudicaudata* Geoff.
b. — *Phalanger celebensis* Gray.
c. — *Tarsipes rostratus* Gerv. & Verr.
d. — *Sminthopsis murina* Waterh.
e. — *Antechinomys laniger* Gould.
f. — *Phascolomys latifrons* Owen.
g. — *Perameles doreyana* Quoy & Gaim.
h. — *Peragale leucura* Thos.
i. — *Hypsiprymnodon moschatus* Rams.
j. — *Macropus sp.*

Figs. a–i after Dollo.

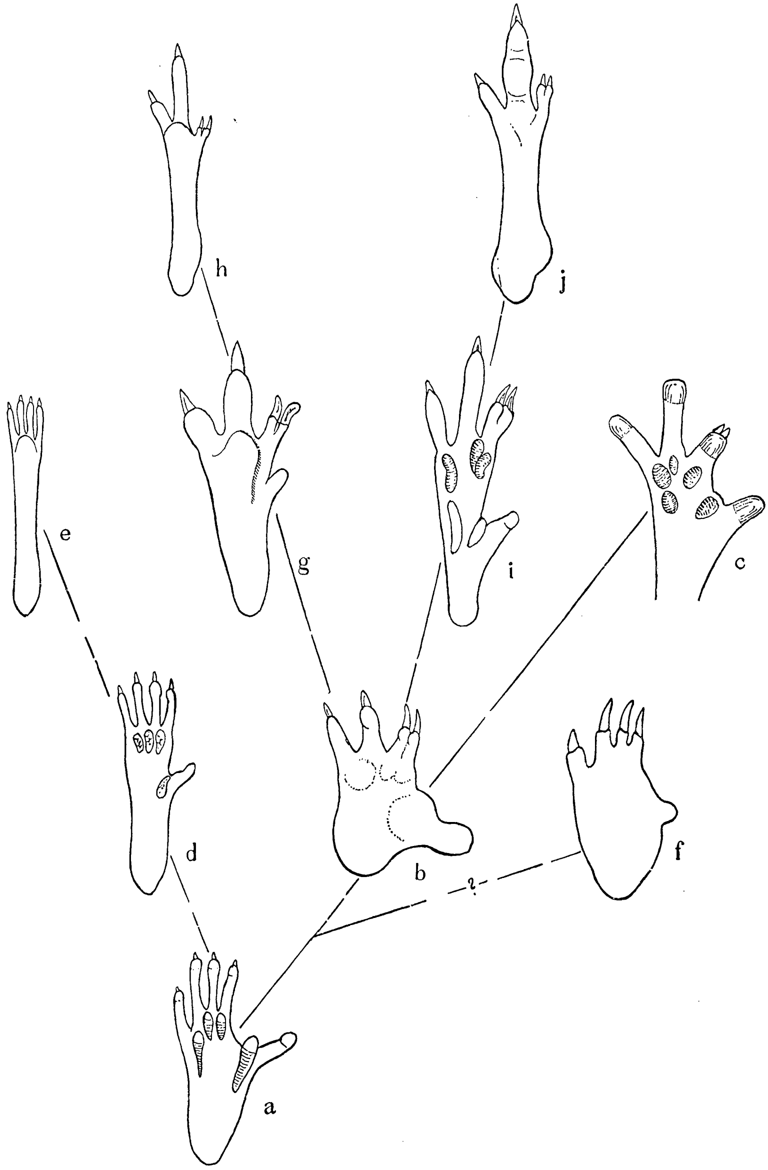

PLATE III.